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Introduction

In an evergreen tropical forest, one might expect that food for leaf-eaters is available in large quantities throughout the year. However, not all leaves are suitable as food. Many folivores feed primarily on young

leaves which contain a maximum of protein and a minimum of lignocellulose and toxic secondary compounds. To estimate the food actually available to folivores, it is necessary to study the leafing phenology and distribution of the many species of rain forest plants.

The evergreen forest of Ipassa (Figure 1) which is 10 km south of Makokou, Gabon, at an elevation of 500 m, was studied in 1971–1972 and in 1975 from a floristic and ecological point of view. Phenological data on tree and liana species were completed by a quantitative study of litter-fall. Leaves of all the species in the litter collected were identified, so as to obtain a quantitative and phenological analysis of the leafing characteristics of the different species. The climate at the Ipassa field station is characterized by a major dry season during which the sun rarely shines and the average temperature is at a minimum of about 21° C. Consequently, there is a minimum of evaporation in this dry season. The average yearly rainfall is 1700 mm. The four equatorial seasons are shown in Figure 2 with more detailed data concerning our main period of study:

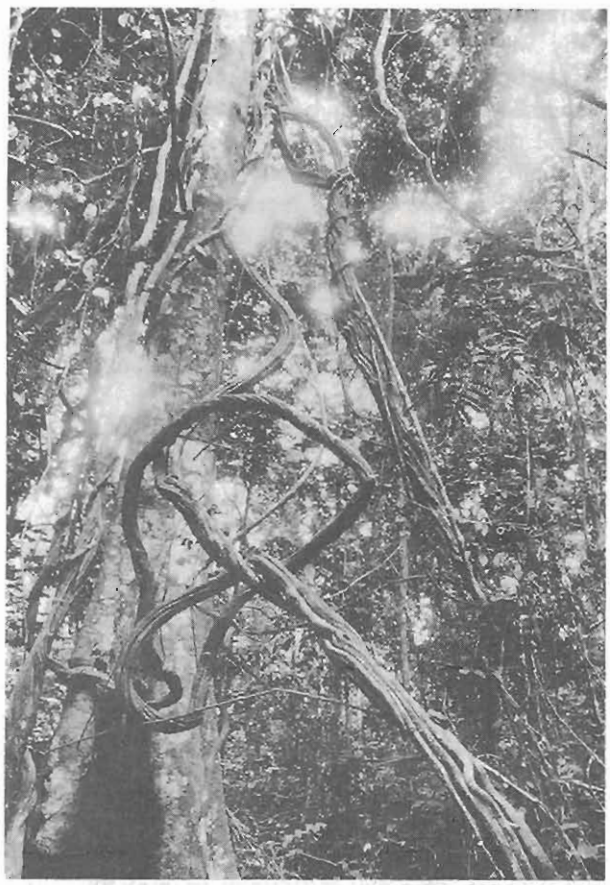

Figure 1. A view inside the rain forest at Ipassa showing the importance of lianas in the forest structure.

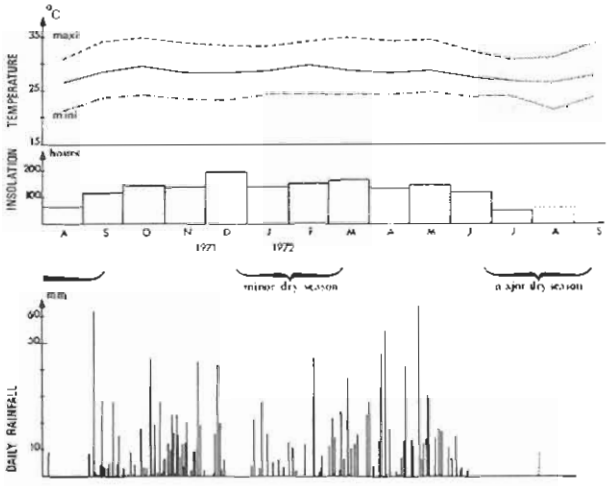

Figure 2. Data from the meteorological station of Makokou concerning the main period of phenological observations. Temperatures are monthly means (broken lines show maxima and minima). Insolation is the total time of bright sunshine per month. The records of daily rainfall show the different patterns of distribution during the rainy season and total absense of precipitation during the major dry season (also characterized by minimum insolation and minimum temperature).

(1) June-July-August (approximately): major dry season with no rain, minimum insolation, minimum temperature, and minimum evaporation.
(2) September-October-November: major rainy season with maximum rainfall and average insolation.
(3) December-January-February: minor dry season with low rainfall and maximum insolation.
(4) March-April-May: minor rainy season with important rainfall and tropical storms, and average insolation.

The temperatures shown (Figure 2) are from the Makokou meteorological station at the airport. In the forest, the vegetation has an important buffering effect. The maximum daily variation above the canopy is 10°C to 14°C while near the forest floor it is no more than 2°C to 6°C, with a gradient of vertical variation. Relative humidity may be less than 50 percent above the canopy but never less than 80 percent in the forest (Cachan and Duval, 1963, in Ivory Coast). The average relative humidity is 96 percent at the meteorological station and, thus, higher inside the forest.

In its structure and floristic composition, the Makokou forest does not differ from other rain forests of the Congo-Guinea block, though rainfall there often is considerably higher. The peculiar major dry season of the Makokou area, with its cool temperature and low evaporation, allows this "rain forest" to grow under relatively dry conditions.

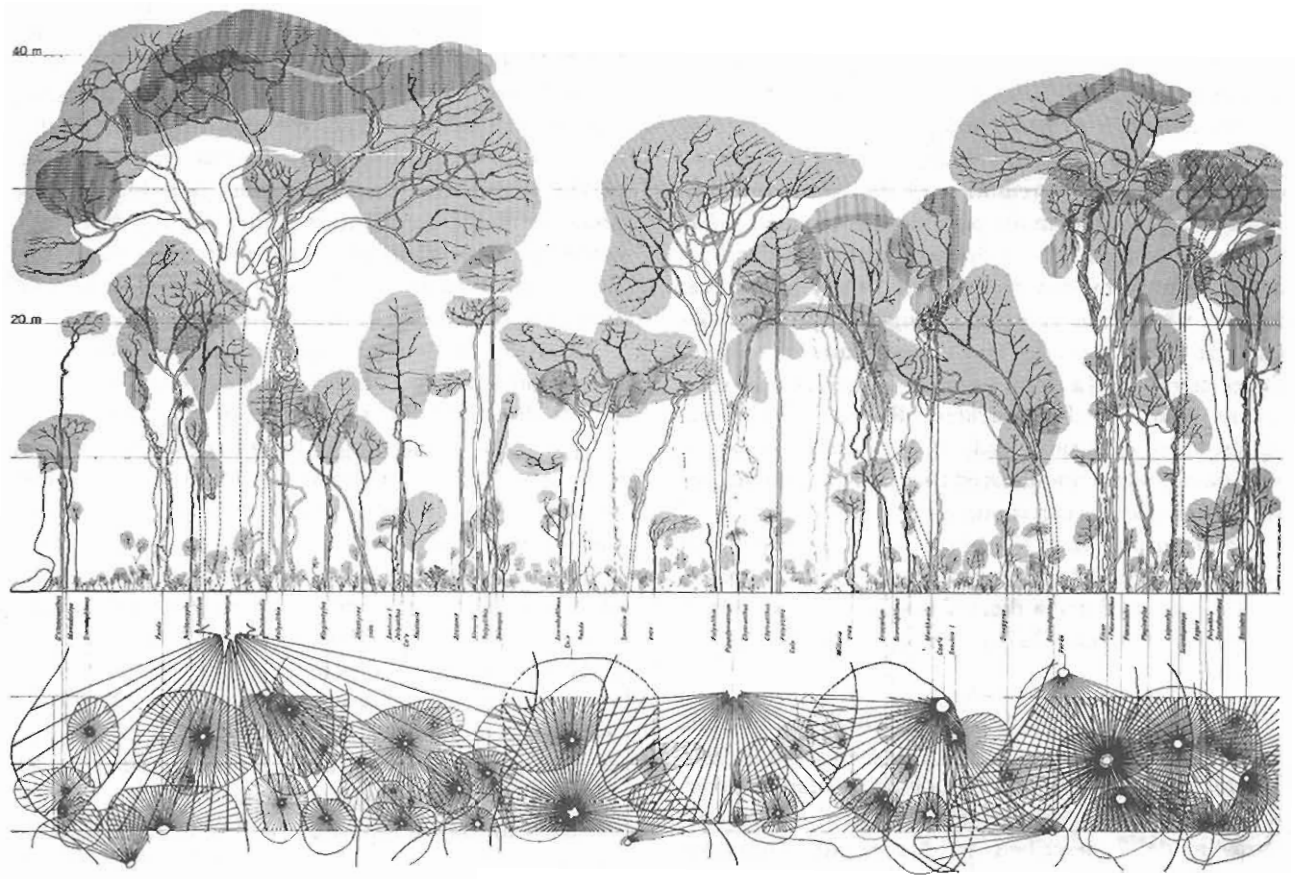

Figure 8. Vertical structure of the rain forest at Ipassa, near Makokou (Gabon), along a transect of 90 by 5 m. Some trunks outside the transect area but supporting a tree crown included in the section are shown in dotted lines. The horizontal structure is shown by the projection of the canopies and trunks in a larger sample area (90 by 10 m) including the strip of 5 m located behind that of the profile. Names of tree species: *Afrostyrax lepidophyllus, Alstonia congensis, Anonidium mannii, Beilschmiedia* sp. (= 1449), *Calpocalyx dinklagei, Chytranthus talbotii, Cola rostrata, Coula edulis, Diospyros hoyleana, Distemonanthus benthamianus, Eriocoelum macrocarpum, Fagara macrophylla, Ficus* sp. (= 1744), *Heisteria parvifolia, Maesobotrya* sp. (= 2111), *Markhamia sessilis, Milletia mannii, Panda oleosa, Pentaclethra eetveldeana, Petersianthus macrocarpus, Piptadeniastrum africanum, Plagiostyles africana, Polyalthia suaveolens, Santiria* sp. I, *Santiria* sp. II, *Scorodophloeus zenkeri, Sorindeia nitida, Trichoscypha* sp. (= 1447). Only generic names are written on the projection; canopies of lianas are represented by hatched areas on the profile.

Forest Structure

The study area is located in ecological quadrats (100 by 100 m) at Ipassa. No attempt was made to analyze either the riparian forest or the periodically flooded forest.

Vertical structure

A vertical profile along a 90 m transect, 5 m wide, in the Ipassa forest was constructed. Some trunks outside the transect area but supporting a tree crown included in the section are shown in dotted lines in Figure 3. We measured the height of trees, lianas, and limbs by using long poles placed on tree trunks. Some trees were climbed, and the main forks and parts of the canopy were accurately measured (optical instruments were useless in this type of forest).

Considering this small and detailed sample of the Ipassa forest alone, there is no obvious stratification (Figure 3). The crown of an emergent, *Piptadeniastrum africanum*, was between 25 and 45 m, two other dominant trees were lower: a *Piptadeniastrum africanum* of 20 to 35 m and a *Ficus* sp. (# 1744) 30 to 40 m, which grew on a *Petersianthus macrocarpus* tree which was reduced to a few branches and small crown. Under these three large crowns, there were many types of combinations, such as a *Beilschmiedia* sp. (# 1449) and *Scorodophloeus zenkeri* mixed with

Fagara macrophylla, all with crowns about 30 m high, and *Markhamia sessilis*, *Coula edulis*, and *Polyalthia suaveolens* with crowns 20 to 30 m high. In the middle of the profile, *Panda oleosa* covers some other crowns although all of its foliage lies between 20 and 30 m. There is a size-distribution among lower trees depending on the distribution of the dominant ones which capture the main part of the incident solar energy. The idea of well-defined strata has been recently refuted by different authors. Only in tropical forests, where one or more strongly limiting factors (such as flood, altitude, and temperature, or soil) reduces diversity to a small number of species, can consistent strata be demonstrated. Rollet (1974) made an extensive statistical study of Venezuelan-Guianese rain forest, and demonstrated that there are no height-frequency classes corresponding to strata.

To generalize as to the whole rain forest from that which has been briefly shown by the above example, we have to consider a dynamic point of view, clearly stated by Oldeman (1975). The trees can be divided into three sets:

(1) The "set of the future" including trees still possessing a potential for future development ("biologically young"), whose branching is mainly determined by an inherited pattern (one of the "architectural models" described by Halle and Oldeman, 1970). These trees are suppressed and their growth is very slow. We may suppose that they cannot produce much food for folivores.

(2) The "set of the present" including all trees which have attained their maximal dimensions intercepting a large part of solar energy, and showing a branching pattern that is mainly determined by prolific reiteration of the hereditary growth model, e.g., not from seeds but from buds. Trees of the present are often to be found at distinct levels, each of which is called a "structural ensemble" by Oldeman (1974). The highest structural ensemble forms the forest canopy. The growth of this set of trees is the fastest, thus we can expect these to have the largest mass of leaves available for folivores.

(3) The "set of the past" includes damaged or decaying trees without either future potential for development or competitive efficiency, destined to be eliminated from the forest. Nevertheless, many of these damaged trees are leafing out of season (for example, just after a large branch has been broken) and thus this set might represent a valuable complement for folivores.

The main ecological difference between the set of the future and the set of the present is an inversion of light and atmospheric moisture conditions. The set of the present intercepts the better part of the light and, under its cover, the high hygrometry and low light are the conditions of survival for the "trees of the future." As soon as the equilibrium is disrupted, e.g., by the fall of a tree, the surviving trees of the future start expanding their crowns by reiteration of the hereditary growth pattern from buds, in a phase of fierce competition. The winning trees become the new "trees of the present;" the losers reduce their volume by shedding branches and may survive again as trees of the future or may die.

Thus the fundamental pattern of the rain forest is not homogeneous but heterogeneous. Aubréville (1938) described the rain forest of the Ivory Coast as a "mosaic" determined by its regrowth, tree by tree. The basic idea seems to be correct, but the surfaces of simultaneous development are larger than the surfaces covered by a single tree. A falling tree most often clears rather extensive surfaces, where more than one other tree can grow. On such a surface, according to Oldeman (1975, manuscript), there is a succession of phases, including slow growth which is regulated by trees of the present. Old, well-structured phases, generally called "mature" forest, do not constitute more than an estimated 5 to 10 percent of the total forest (Oldeman, 1974).

Mixed in the canopy is the foliage of many species of lianas. They form a very important part of the total forest leaf biomass (at least 36 percent, A. Hladik, 1974), but their growth and population dynamics are still subject to study. They have the tendency to overgrow in any place where enough light is available. They seem to accompany the supporting trees during their growth upward, i.e., they generally do not climb toward the forest canopy along old trunks (Oldeman, 1974). They usually survive tree falls, and form the oldest and most diverse components of some forests (Montgomery, Sunquist, and Croat, in press).

In such a dynamic environment the classic notion of strata does not apply and the notion of ecotope has to be considered instead: it represents the plant, species or individual, and its feedback into its own environment. Ecotopes form various volumes distributed at different heights. Their places are related to the horizontal structure of the forest.

Horizontal structure.

In a plot of 900 m^2 (90 $\times$ 10), the projection of the canopy from a top view was drawn (Figure 3) with the help of a plumb line to determine the contours. The cross-sectional area of the crown of all trees over 10 cm diameter (35 individuals of 23 species)

is 1640 m^2. In this sample, the large trees of the set of the present (4 individuals of 3 species) total 835 m^2. This is about half of the total of all trees. In an area of Barro Colorado Island used by radio-marked sloths, total cross section of trees over 15 cm diameter was about 35,000 m^2 per hectare and about 12 percent of the trees had crowns with cross-sectional areas greater than 20 m^2 (Montgomery and Sunquist, 1975, 1978). The leaf biomass of a tree is proportional to the cross-seetional area and to the height of the crown. Moreover, for each speeies it also depends on a factor of density of the foliage, and we noticed that many emergent trees have tiny leaflets (for example, many trees of the Leguminosae family, such as *Piptadeniastrum africanum*). With this restriction for a correet estimate of the leaf biomass, we can assume that few speeies account for a large part of the leaf biomass in a localized plot.

On a larger scale it is not possible to calculate the area of the crowns. The species diversity is better demonstrated by the number of tree boles (Table 1). The trees over 5 cm diameter on a plot of 0.4 ha belong to 95 different species. However, large trees (over 60 cm diameter) include few species. As the plot increases in size, the number of species of large trees becomes higher with 60 species for 20 ha following a rapid estimation over the total study area at Ipassa.

Considering only this increasing diversity of tree species as the plot increases in size, this African forest seems approximately as rich as the American rain forest (according to Rollet, 1969, there are 68 species over 60 cm diameter for 16 ha in Guiana and a total of 365 species of trees and lianas over 10 cm diameter in 64 ha). On the regional scale (northeast of Gabon), one might expect to find a total of perhaps 4,000 plant species.

There are few data concerning the distribution of lianas and the shapes of their crowns, owing to the difficulties of observation and field identification. The shape of the most obvious masses of liana foliage are roughly localized on the profile (Figure 3). Liana-leaf biomass is about one-third of the tree-leaf biomass and speeies diversity is unknown but obviously important. There are 33 identified species of lianas for 57 species of trees along two transects of 200 m each (A. Hladik, 1974). Montgomery and Sunquist (1978) identified a total of 28 liana speeies from 13 trees used by sloths on Barro Colorado Island. They examined 39 trees of which 11 had no lianas in their crowns. The remaining 28 trees contained a total of 55 liana species.

The distribution of one species of liana, *Entada gigas*, has been mapped at Ipassa (Charles-Dominique, 1977). A corresponding map of the unequal distribution of a nocturnal Prosimian, *Euoticus elegantulus*, shows that the animals are distributed exactly according to the unequal distribution of the lianas from whose stems they eat gum. It is exceptional though that the distribution of one vertebrate species can be related only to one plant species.

In the rain forest, the great diversity of tree and liana species, the low density of most of the species, and the many ways they can be distributed horizontally and vertically to form different ecotopes allow a great number of animal species to be specialized in particular niches. The distribution of the birds in thc various ecotopes of the Ipassa forest is presently under investigation by Erard (personal communication). According to his field observations, the Muscicapidae spend most of their time in areas that vary from species to species. Such factors as branch density, which are not related to the notion of strata, determine species habitat preferences.

Five species of nocturnal Prosimians have been studied by Charles-Dominique (1971, 1977), who recorded on each occasion the types of branches and lianas on which the animals were first observed. The Angwantibo, *Arctocebus calabarensis*, uses the

Table 1.—Densities of tree species compared to number of individual trees in different plots at Ipassa (10 Km South of Makokou) and Bélinga (70 Km North of Makokou); data for Bélinga are taken from Le Thomas, in Aubréville, 1967.

	Diameter ≥ 5 cm		*Diameter ≥ 10 cm*		*Diameter ≥ 30 cm*		*Diameter ≥ 60 cm*	
Location and size of plot	*Species*	*Individuals*	*Species*	*Individuals*	*Species*	*Individuals*	*Species*	*Individuals*
Ipassa 0.4 ha	95	304	62	171	22	47	5	9
Ipassa estimate /ha		760		427		117		22
Bélinga 1.0 ha		789		495	50	119	14	22
Ipassa 0.9 ha					36	86	13	22

ecotope composed of thin lianas and thin branches developed around the decaying trees of the set of the past and in small clearings where vegetation is growing fast. Feeding essentially on caterpillars, this animal is a limiting factor on the population of folivorous insects of this particular ecotope. The potto, *Perodicticus potto*, lives in more open places and travels on the branches on top of trees of the set of the present. It feeds partly on folivorous insects. Allen's bushbaby, *Galago alleni*, also feeds partly on insects (and fruits), but this vertical leaper is found only on the vertical small trunks of the set of the future and on liana stems. This ecotope is characteristic of large areas near the ground of the rain forest and may also extend to some height near the tree tops. Demidoff's bushbaby, *Galago demidovii*, inhabits the volume of thick foliage and twigs enveloping large and small trees. It is also an insect feeder not competing with any of the previous species because it forages in a different ecotope. The fifth species of Prosimian of the Ipassa forest is the needle-clawed bushbaby, *Euoticus elegantulus*, which has the particular distribution described above. Because of its anatomy, *Euoticus* can move along the largest smooth trunks and branches and, thus, it is present in the most open volumes of the forest.

The zoological studies of P. Charles-Dominique introduced a practical aspect to the notion of ecotope which might slightly differ from a botanical point of view confined to studies of plant species. The forest structure is divided into different volumes for which height and localization are not correlated. The type of ecotope in each of these volumes is related to the dynamic structure of the forest (evolution of "sets" as proposed by Oldeman), but not to a theoretical notion of strata that have never been demonstrated in a rain forest. The colonization of different ecotopes by different vertebrates is the best demonstration of the validity of this view; but further botanical and zoological investigations are necessary to add precision and, eventually, to normalize the definitions.

The folivorous mammals at Ipassa are poorly known or absolutely unknown. The Colobidae and the Gorillas were only occasionally observed. Other primates show a tendency for folivory, especially *Cercopithecus nictitans* (Gautier-Hion and Gautier, 1974). To a lesser extent, chimpanzees also eat leaves (C. M. Hladik, 1973). The other arboreal folivores are Anomalurids (scaly-tailed flying squirrels) and the tree hyrax (*Dendrohyrax dorsalis*) of which we know very little.

Generally speaking, the folivorous mammals have small home ranges and a large part of their food is taken from a small number of tree species. For instance, the sloths of America (Montgomery and Sunquist, 1975, 1978) used "modal trees" on which they spent a large part of their activity.

In Asia and East Africa, the leaf monkeys living in a semideciduous forest feed on a limited number of tree species (Hladik and Hladik, 1972; Oates, 1974; Struhsaker and Oates, 1975). If folivorous species feed selectively on a small number of tree species in the rain forest, home ranges would necessarily be larger because of the dispersed distribution of the plant species. This seems corroborated by the observations on *Presbytis senex* in the Sinaradja forest in Sri Lanka (Hladik and Hladik, 1972). Superficial observations (location of the groups according to the calls) indicate that the group home range is about six times the size of that of the same species living in drier forests. In a species-rich forest, it is likely that different groups of the same folivorous species eat different species of leaves as staple food. Different folivorous arboreal species might be expected to be adapted to different ecotopes, as in the case of the other mammals.

Phenology of Leaf Production

Measures of litter fall

Total litter production at Ipassa between July 1971 and July 1972 was 13.3 T/ha/year, which is comparable to litter production in other rain forests (Table 2). We collected litter from 120 sampling baskets of corrugated sheet metal, each about 0.8 m^2 (total 95.4 m^2), placed 10 meters apart in line along two 600 m transects. Litter was collected from the baskets every 2 weeks (or 3 weeks during dry periods). It was dried to constant weight in an open electric dryer. The loss of litter weight due to the stay in the sampling baskets was calculated: 3 samples of litter were dried in an oven (90° C) and returned to 3 sampling baskets in the forest for 2 weeks during a period of heavy rain. They lost 6 percent of their weight. Considering that in the open dryer 5 percent of humidity is retained (by weight), our data can be considered as the correct dry weight ± 1 percent.

The litter was analyzed by sorting out leaves, fruits, flowers, wood, and "dust." The dust included decomposed wood and bark, pieces of leaves and flowers, and various unidentified materials. Large leaves were usually in good condition, except when eaten by insects. In the case of large compound leaves, we sometimes separated only the leaflets without petioles and petiolules. In the case of small leguminous leaflets, we did not take time to weigh them

Table 2.—Comparative litter production of different forests in the world.

Country	*Types of forest*	*Litter production T/ha/year*		*Reference*
		Leaves	*Total*	
France	Temperate deciduous forest (*Fagus sylvatica*)	2.8	5.9	Lemée and Bichaut, et al. (1971)
France	Temperate evergreen forest (*Quercus ilex*)	1.6 to 3.4*	3.1 to 4.7	Rapp (1969) on 4-year study
Ivory Coast	Woodland savanna	1.8		Menaut (1974)
Sri Lanka	Semiarid semideciduous forest	—	3.9	Hladik (in prep.)
Sri Lanka	Dry semideciduous forest	2.4	4.6	
Ghana	Tropical semideciduous forest	7.4	9.7	John (1973)
Panama	Tropical semideciduous forest	6.0 to 7.0	11.4 to 12.6	Foster; Smythe (1974, unpublished manuscript) on 2-year study
Ivory Coast	Tropical evergreen forest-Banco	7.3 to 9.2	9.0 to 13.4	Bernhard-Reversat (1970) on 2-year study
Ivory Coast	Tropical evergreen forest-Yapo	5.7 to 7.6	8.3 to 10.1	
Gabon	Tropical evergreen forest	6.5	13.3	Hladik (present paper)
Malaya	Tropical evergreen forest	7.5	10.0	Lim (1974)
Sri Lanka	Montane evergreen forest	3.5	5.9	Hladik (in prep.)
India	Montane evergreen forest	2.4 to 5.0**	3.8 to 7.3	Blasco and Tassy (1975) on 3-year study

* There is a biannual variation of the leaf production: the average is 2.5 T /ha /year.
** This large annual variation might be due to the sampling method.

when they occurred in small quantities. Fruits and seeds were easy to recognize, but flowers sometimes were included in the "dust." Wood included all pieces of wood which fell into the sampling basket except for a huge mass of lianas and one small trunk which fell on a basket. The fall of trunk was statistically very rare and was not included here in the total litter fall. Quadrats larger than 100 m^2 are necessary for measuring total wood fall.

All macroscopic insects and other invertebrates were collected before each collection of litter. We obtained a total of 2.3 g/m^2/year (dry weight). A maximum of "insect production" occurred during the end of the major rainy season and the minor dry season. Charles-Dominique (1971), collecting insects in light traps at night, obtained a maximum of moths in April. This suggests that caterpillars were abundant at a period corresponding to our maximum of "litter insects." Many of these insects (caterpillars and grasshoppers) are folivores and grow during the period of leaf flushes.

Leaf-fall

Leaves from 40 of the 120 baskets (in a line of 400 m) were weighed with a minimum of manipulation. We obtained 6.5 T/ha/year of leaves for 13.9 T/ha/year of total litter fall (i.e., 47 percent). Leaves from 40 other baskets were identified to species before weighing (A. Hladik, 1974). Because identification involved frequent manipulations and some damage to leaves, a larger proportion of dust from the leaves was obtained.

Leaf-fall is more regular throughout the year than total litter fall (Figures 4 and 5). Leaf-fall reached a conspicuous low point of 1.2 g/m^2/day in June and July, during the major dry season. It reached a small peak of 2.0 g/m^2/day in September during the major rainy season, and a higher peak of 2.8 g/m^2/day in March and April during the minor rainy season. The total litter fall reached its annual maximum in the minor rainy season with 10.5 g/m^2/day because many twigs and decaying wood fell during storms.

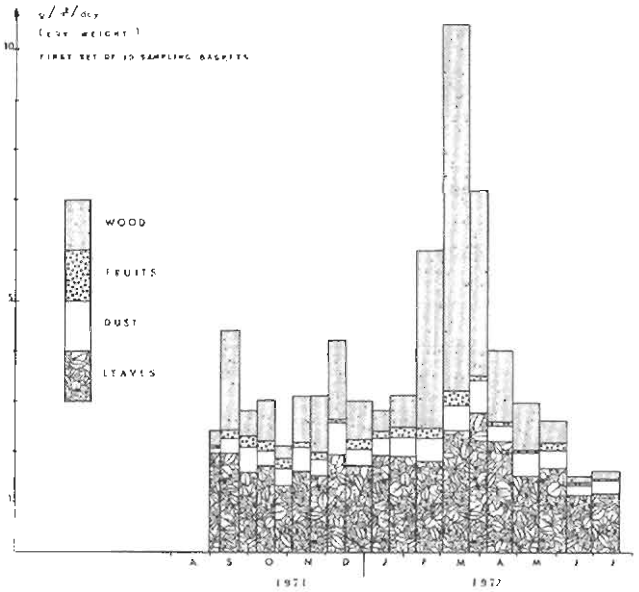

Figure 4. Seasonal litter-fall production is 40 sampling baskets (32 m^2) on a 400 m long transect at Ipassa ($g/m^2/day$).

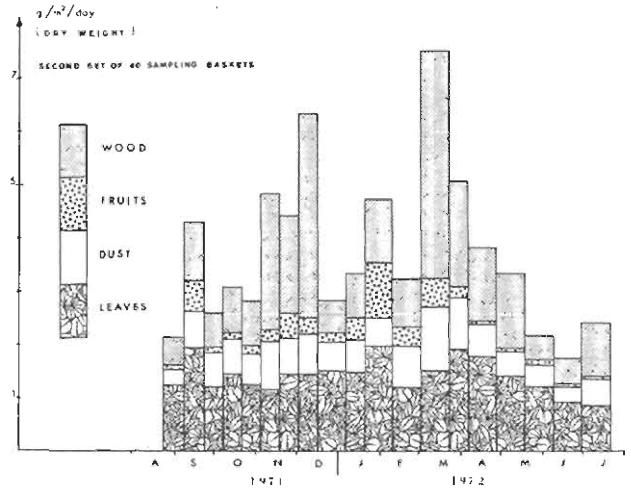

Figure 5. Season litter-fall production in the second transect at Ipassa. The "dust" fraction in these samples is more important compared to Figure 4 due to the method of analysis (see text).

The small peaks in our leaf-fall graphs correspond to the shedding of leaves by deciduous trees, e.g., two in March and April (*Berlinia bracteosa* and *Parkia bicolor*; Figure 4) and one in January and February (*Piptadeniastrum africanum*; Figure 5). These irregular peaks are related to the number of deciduous trees included in the transects.

Lianas contributed a large part of the leaf biomass (Hladik, 1974), and the relative leaf-fall from lianas and trees was: lianas, 36 percent; trees, 59 percent; unknown species, 5 percent, which probably included more lianas than trees. With the exception of one small peak between September 9 and 24 (Figure 6), the total leaf-fall of lianas was more regular than that of trees, but some individual liana species showed a seasonality in leaf-fall.

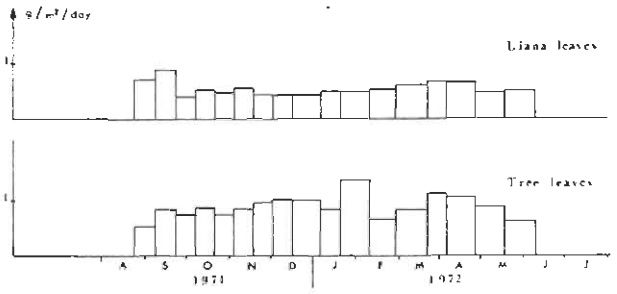

Figure 6. Comparative seasonal leaf litter-fall for trees and lianas at Ipassa ($g/m^2/day$).

Phenological sequences of trees

To complement the measures of litter-fall, direct observations of leaf-fall, leafing, flowering, and fruiting of 300 labeled trees along 4,000 m of trail were made at intervals of 2 to 3 weeks in 1971–1972 and 1975. The difficulty in quantifying new leaf production over these standing trees in the forest allows us to take notice of only peaks of production. Flushes[1] of numerous new leaves are obvious in the tropics because these leaves are very often bright or dark red (as previously mentioned by Richards, 1952) or at least light green.

The observations of phenological events have been combined with data on leaf-fall for a number of important species on the transects (Figures 7, 8, 9, and 10). There are three main types of phenological sequences with respect to leaf-fall. The first, illustrated by *Piptadeniastrum africanum* and others (Figure 7) occurs when the leaves fall during a fairly short period once each year (or without annual cycle) and the trees remain bare for a few days or more. These trees are called deciduous. The second type, illustrated by *Panda oleosa* and others (Figure 8), occurs when leaf-fall comes in peaks with concommitent flushes of new leaves. In the third type, leaf-fall is more or less continuous throughout the year, with a general

[1] "Flushes" is used here as an expression of bunches of new leaf growth obvious from observations with binoculars. In fact, leaf flush might be related only to endogenous rhythmic growth which appears to be common for many tropical plant species, but not all (cf. work on the periodicity of tree growth by Koriba, 1958).

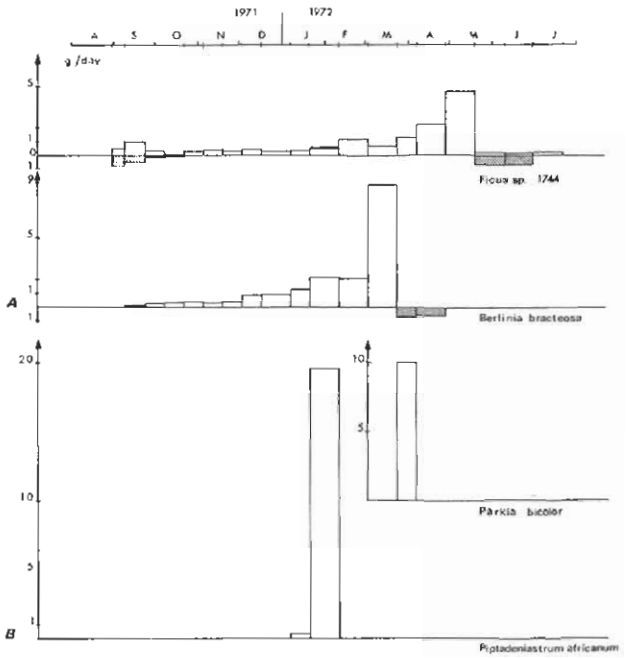

Figure 7. Phenology of deciduous trees. A = Quantitative estimate of the leaf production of two emergent trees at Ipassa as indicated by the dry weight of their deciduous stipules falling in 40 sampling baskets (shaded areas). The leaf-fall (clear areas) occurs in large quantities during a short period. B = The important and sudden leaf-fall of two leguminous trees (dry weight in g/day in the 40 sampling baskets).

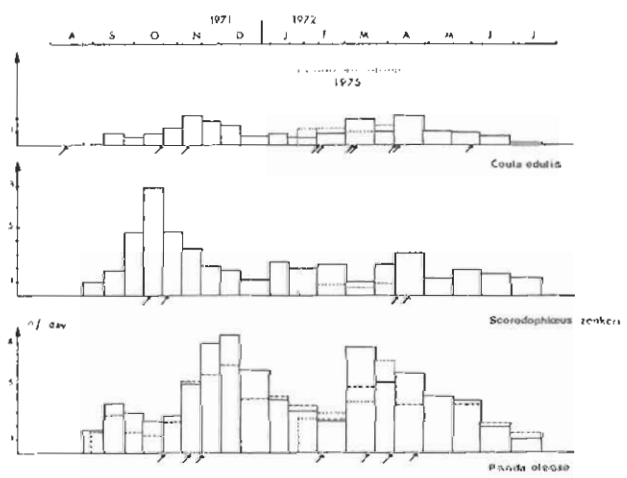

Figure 8. Seasonal leaf-fall in g/day in 40 sampling baskets and leafing times (arrows) of some important tree species of Ipassa. The dotted lines show the observations during 1975. For *Panda oleosa* leaf-fall production in the first set of baskets is compared to leaf-fall production in the second set analyzed (dashed lines).

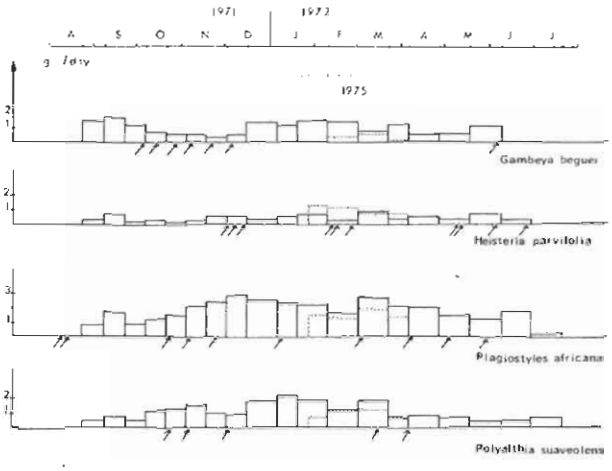

Figure 9. Seasonal leaf-fall in g/day in 40 sampling baskets and leafing times (arrows) of some common and one emergent tree species at Ipassa (dotted line is data taken in 1975).

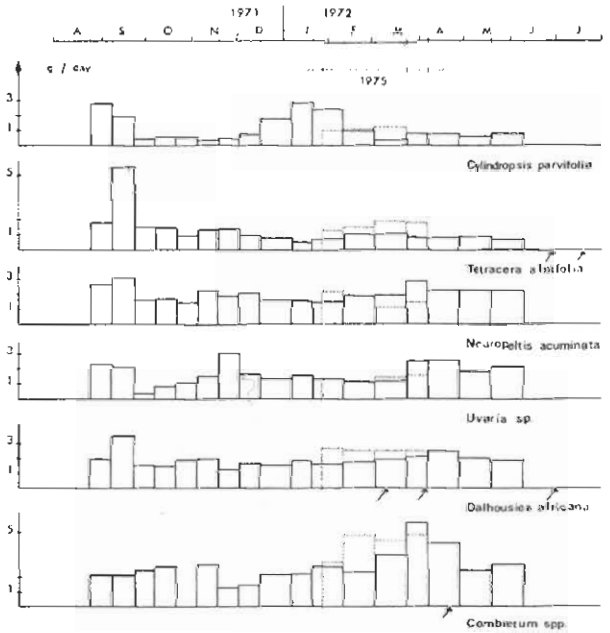

Figure 10. Leaf phenology of the most important liana species (leaf-fall over 10g/m^2/year) in the analyzed leaf litter (40 sampling baskets). Dotted line is data taken in 1975. The most obvious leafing times (arrows) have been noted only for three species.

decrease in leaf-falling during the major dry season, and is illustrated by *Polyalthia suaveolens* and others (Figure 9). In these last two types of evergreen trees, leafing periods often correspond to rainy periods. A general survey is presented for the most important species (by weight in our baskets) including numerous individuals of a common species or one individual of a rare emergent species.

The emergent trees of our transect, which had large crowns, were responsible for a large part of the total leaf biomass. One huge strangling fig, *Ficus* sp. (1744), demonstrates the phenology of a deciduous tree in the tropics. Leaves start to fall in February with a peak at the beginning of March (Figure 7), then new leaves appear immediately and last for about a month. *Ficus* has deciduous stipules, and it was possible to measure the intensity of new leaf production by weighing the fallen stipules. The phenology of the genus *Ficus* is singular with two periods of fruiting (or even three) elsewhere in the world. It seems, however, to be different in Gabon where figs are not so abundant and a special study on *Ficus* sp. is in progress. *Berlinia bracteosa* (Figure 7) has deciduous stipules during the leafing period which follows leaf-fall in March. These trees with falling stipules are interesting because they allow the collection of quantitative phenometric data of new leaf production which are otherwise so difficult to estimate. Another species in our transect, *Piptadeniastrum africanum*, is deciduous (Figure 7). Leaves fell during a very short period which was followed immediately by several days of leaf production. For the tree shown (Figure 7), this occurred between January 7 and 21, hut all the individuals were not synchronous with respect to leaf phenology (Figure 12). One *Parkia bicolor* tree showed the same rapid leaf-fall between March 24 and April 7 (Figure 7). New leaves appeared shortly after leaf-fall. Nevertheless, some other emergent large trees were not deciduous, c.g., *Gambeya beguei* (Figure 9) which had regular leafing and leaf-fall periods all the year.

The more common medium-size trees on our transect had a variety of leaf phenology patterns. The most common species were *Panda oleosa* with 10 trees (over 30 cm diameter) per ha, and *Scorodophloeus zenkeri* with 16 such trees per ha. Both are generally medium-size trees growing to 30 m high. The leaf-fall of *Panda oleosa* appears to be bimodal with peaks in November-December and March-April (Figure 8). New leaves appear before old leaves fall, and keep growing for some weeks during the rainy season. Leaf-fall of *Scorodophloeus zenkeri* (Figure 8) shows one peak earlier in the rainy season, in October. This species, however, has two leafing periods in October and April. *Coula edulis* with 4 trees per ha, is a medium-size tree whose leaf-fall seems bimodal, with perhaps additional leafing periods (Figure 8). The leaf-fall of *Coula* studied in the Ivory Coast (Bernhard-Reversat, 1970) also showed two peaks more or less distinguishable. *Polyalthia suaveolens* with 6 trees per ha, and *Plagiostyles africana* with 7 trees per ha are also medium-sized trees. Their leaf-fall appears more or less continuous (Figure 9) with two principal leafing periods for *Polyalthia*, contrasting with *Plagiostyles* which has new leaves many times during the year even including the dry season. *Heisteria parvifolia* with 2 trees per ha also has new leaves in the major dry season as well as the rainy season (Figure 9) although there is continuous leaf-fall.

Phenological sequences of lianas

The study of leaf litter-fall of lianas gave some interesting quantitative information although phenological events were directly observed for only a small number of species owing to the difficulty of recognizing individual lianas. The continuous total leaf-fall of lianas (Figure 6) is the result of varying seasonal production of different species (Figure 10).

Cylindropsis parvifolia and *Tetracera alnifolia* show a clear seasonality in leaf phenology. Other species like *Neuropeltis acuminata* and *Dalhousiea africana* show irregular leaf production without large peaks. The 1975 data indicate possible annual variations in leaf-fall production but probably with a similar seasonal pattern. The leafing periods precede the leaf-fall periods for *Dalhousiea*, but followed it for *Combretum*. For some lianas, such as for *Tetracera* and *Dalhousiea*, new leaves occurred during the major dry season.

Leaf Phenology and Food Availability

The total leaf-fall pattern of the Ipassa forest, examined by the method of weighing litter in several traps, shows only small annual variations (except a minimum during the major dry season). The specific leaf-fall cycles of some liana species, some common tree species and the emergent trees of our transect have been pointed out as partly complementary. Leaf flushes were recorded by direct observation, and in a few cases after precisely weighing the deciduous stipules. The sample on which species-by-species leaf analysis was carried out includes 18 common tree species, 2 deciduous emergent trees, and 1 evergreen emergent tree, corresponding to 70 percent

Table 3.—Estimate of the annual distribution of leaf production of some important tree species.

The total dry weight obtained on 31.8 m^2 of 40 sampling baskets has been partitioned into periodical production for each leafing period. The monthly numbers represent the future production of mature leaves (g by dry weight) in relation to the intensity of leafing. The young leaves available each month can be roughly considered as 1/10 of those weights. (During August new leaves were rare; in September we had no precise data).

	Monthly leaf production (by dry weight, on 31.8 m^2)									
Species	*O*	*N*	*D*	*J*	*F*	*M*	*A*	*M*	*J*	*J*
Panda oleosa		600			300	200	200			
Scorodophloeus zenkeri	450						300			
Plagiostyles africana	60	100		60	60	60	60	60	60	
Coula edulis	50	50			80	80	80	50		
Polyalthia suaveolens	70	70	70			70	70			
Macaranga barteri		50					200		50	
Santiria sp. II	30	30	10	40	30	10	50	60	30	
Santiria sp. 1					30	30	10		30	
Petersianthus macrocarpus	40	100	30	20	30	20	10		30	10
Pentaclethra eetveldeana		75	75	30						
Pausinystalia macroceras			100				60			
Heisteria parvifolia			40		40			25	15	15
Ficus sp. 1744								250	80	
Piptadeniastrum africanum					400					
Gambeya beguei	100	100								
Total future production of mature leaves	800	1175	325	150	970	470	1040	445	295	25
Estimate of young leaves available	80	120	35	15	100	50	100	45	30	3

of the total tree leaf-fall (in dry weight, A. Hladik, 1974). We estimated the monthly available new leaves on this particular sample by dividing the annual dry weight of leaf-fall (for each species) in several fractions proportional to the importance of each leafing period. Thus, the monthly weight (Table 3) is the potential dry weight of mature leaves to be produced at each leafing period of each species. The dry weight of available young leaves during the period of production is about one-tenth of this number. This estimation gives the relative values of leaf production among various tree species, their variations throughout the year with peaks in November and April, and a rough estimate of food availability. Lianas are excluded, however, because we do not have enough data on their leafing periods and, to obtain an adequate figure, it will be necessary to make a general survey of the forest on a larger sample corresponding to the supplying area of folivorous animals.

As a different method of estimating food availability, we can use our phenological data of 300 labeled trees of about 150 species dispersed along 4,000 m of trails. This sample is not a plot and it does not give quantitative data on leaf production since it has not been related to crown size (and lianas are excluded). Nevertheless, it gives an idea of the variation in young leaves available in different seasons (Figure 11) and it can be compared to other studies on labeled trees. It is noticeable that the annual leafing pattern according to our study (Figure 11)

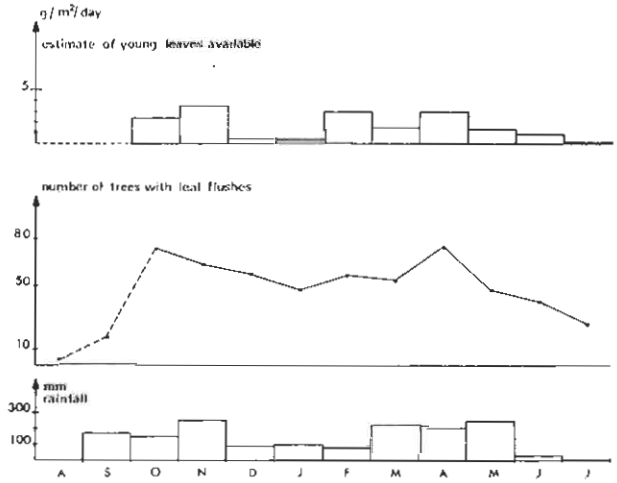

Figure 11. Monthly estimate of young leaves available (after data from Table 3) and number of trees with new leaves among 300 labeled trees at Ipassa. The maximum in October-November and February-March-April occurs when rainfall is maximum.

is similar to the one obtained by the leaf-fall method: most of the new leaves occur at the beginning of the rains that follow the dry seasons. Medway in Malaya (1972) and Leigh and Smythe in Panama (1978) obtained similar results. In Panama, leaf production shows a very high peak in June, after the dry season, and a sharp low in August. This pattern is probably due to the pronounced seasonality of this semideciduous forest, just as leaf-fall is more seasonal in Panama than in the rain forest of Ipassa. Distribution of rain in the tropics generally is quite variable from year to year, and monthly averages do not give enough precision to be correlated with phenological sequences. New leaves may occur just after thunderstorms during the dry season (Hladik and Hladik, 1972). Phenological studies have been conducted in wet and dry forests of Costa Rica (Frankie, et al., 1974). The results (in number of species) are surprising, especially for the wet forest and the riparian forest in the dry zone where most of the leaf flushes occur in the dry season. But what is a dry season? In that wet forest, February and March, the driest months, total each an average rainfall of 200 mm. Nevertheless, rainfall is only one among several climatic factors, and plant growth might be induced as well by temperature or saturation deficit or photoperiod (Catinot, 1970). Moreover, the factors controlling growth may not be the same for all species.

Beside the most common evergreen trees, the deciduous trees of a rain forest play a particular role in the food availability for folivores. Most of them are large emergent trees which suddenly produce a localized mass of young leaves. They may flush at different times of the year (Figure 12) according to the species, and even to different individuals of the same species, as in *Piptadeniastrum africanum*. The percentage of bare trees is only 1 percent at any time. Although the number of large deciduous trees is fairly small (about 2 to 3 per ha), they may be of great interest when growing in the supplying area of a folivore. Of the 21 deciduous species observed, 10 were Leguminosae, of which many species have a high protein level, especially in the young leaves (Table 4). Several times, when the *Piptadeniastrum* tree was leafing, many pieces of young leaves were found on the ground, indicating that folivorous animals had been foraging in the tree. Only 60 percent of the deciduous trees observed in 1971–1972 and in 1975 showed a similar leafless period. During a 6-year study in Malaya, Medway (1972) reported four annually deciduous species and four irregularly deciduous species. In the Cameroun, phenological observations of more than 2,000 trees (about 150 species) were carried out for up to six years under the supervision of Dr. R. Letouzey. These data are presently compiled for an overall study (A. Hladik, in prep.).

Leaf phenology should of course be considered as part of plant physiology and is probably related to the reproductive state of the plant (flowering and fruiting), a topic not discussed in this paper. When a tree is young, it may grow new leaves more or less regularly throughout the year and become deciduous when it is adult (e.g., phenological cycles of *Didymopanax morototoni* in Panama, A. Hladik, 1970). Changes in leaf phenology occur when a tree passes from the set of the future to the set of the present.

From comparative studies on cultivated trees in the tropics, rhythmic or continuous growth can be defined as either endogenous (genotypic) or related to the climate. The growth of some economically important tropical species is well known (for *Hevea brasiliensis*, Halle and Martin, 1968), but we have little knowledge of the growth habits of the various species mixed in a rain forest.

In conclusion, some folivorous mammals which depend mostly on young leaves will be necessarily distributed according to the leaf phenology of many or a few selected species. The deciduous trees offer a brief mass of leaf flushes at various places widely spread through the forest. The evergreen trees represent the remaining stock of young and mature leaves. The density of folivorous mammals might be generally low in relation to a crucial period when few new leaves are available. If folivores are able to utilize mature leaves at this time of restriction, their density may be very high. In the latter case, the problem for folivores is to use the most nutritious species.

Leaves as Nutrient Sources or Repellents

Nutrients

Folivores utilize more shoots than mature leaves, and preferentially eat the shoots and new leaves if, and when, available. This is clear at least among the leaf-eating forms of primates. The nutritional value of the shoots, buds, and young leaves of some trees in Gabon is higher than that of the mature leaves (Table 4). Similar nutritional differences have been shown for some species of Barro Colorado Island, Panama (Hladik, et al., 1971). Some comparative results concerning shoots and mature leaves of different species eaten by the Sri Lanka primates are shown in Table 5.

Primates make many food choices based on positive

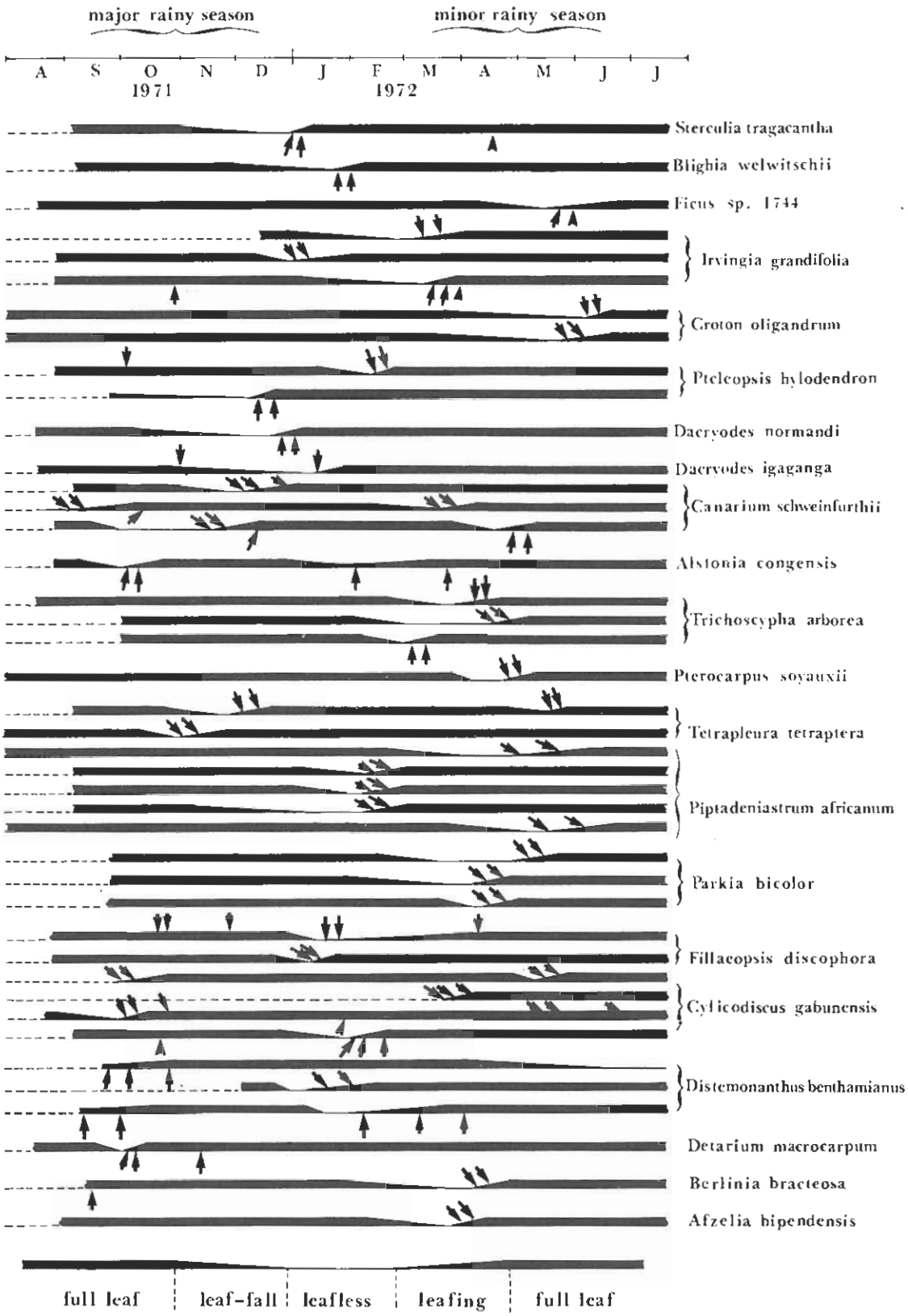

Figure 12. Leaf phenology of deciduous trees at Ipassa. The arrows show the leafing times which follow the period of leaf-fall, or may appear at different times of the year.

Table 4.—Composition of shoots, flushings, leaves, and stems eaten by primates in Gabon.

		Percent of the dry weight					*Parts per thousand*			
Species	*Food*	*Proteins*	*Lipids*	*Reducing glucids*	*Cellulose*	*Total minerals*	*P*	*Ca*	*K*	*Cl (NaCl)*
Baphia leptobotrys	shoots	55.0			12.3	6.4				
	young leaves	36.3	2.25	20.1	14.9	3.7	1.99	2.66	11.79	0.64
	mature leaves	26.1	1.3		36.6	8.9				
n° 1383 (leguminous tree)	young leaves	24.4	1.3	14.5	37.0	4.1	2.18	1.90	14.2	1.58
Newbouldia laevis	young leaves	21.7	4.1		13.8	5.4	2.83	2.21	19.1	
Ongokea gore	shoots	19.3	1.2	24.9	8.9	3.8	2.20	2.22	12.1	
n° 2335	leaves	17.9	1.6	13.3	37.6	5.8	3.66	2.73	21.9	1.94
Dinophora spenneroides (herbaceous plant)	leaves	16.7	10.7	31.1	11.0	3.6	2.03	4.64	17.2	1.50
Cryptosepalum congolanum	young leaves	13.1	0.92	21.3	25.8	3.6	1.97	1.10	11.2	0.97
Cissus dinklagei (liana)	young leaves	10.3	11.2	32.7	11.2	3.4	1.32	6.62	8.8	0.64
Gilbertiodendron dewevrei (not eaten by chimpanzee)	young leaves	10.2	0.7	13.5	46.7	3.9	3.17	4.38	14.1	0.58
Hypselodelphis violacea	stem	5.7	1.1	11.4	51.3	4.9	0.99	2.18	13.8	5.04
Musanga cecropioides	petiole	11.5	0.60	16.9	19.3	17.1	2.62	24.00	54.4	13.40
Pseudospondias microcarpa	petiole	4.8	0.33	28.0	21.3	10.0	0.81	8.0	33.4	3.24

Table 5.—Composition of some shoots, flushings, and young leaves eaten by primates in Sri Lanka.

		Percent of the dry weight					*Parts per thousand*			
Species	*Food*	*Proteins*	*Lipids*	*Reducing glucids*	*Cellulose*	*Total minerals*	*P*	*Ca*	*K*	*Na*
Drypetes sepiaria	shoots	14.74	0.91	9.0	12.7	7.5	3.27	2.7	3.30	0.065
	leaves	7.13	1.28	6.9	30.8	8.8	2.0	10.0	27.0	0.840
Walsura piscidia	shoots	17.79	1.45	5.2	14.8	6.6	2.58	2.29	32.06	0.087
	young leaves	19.52	1.47	8.3	13.6	7.3	3.40	1.65	32.50	0.075
	mature leaves	11.20	4.69	14.4	22.6	6.1	1.25	10.25	18.00	0.087
Manilkara hexandra	flushings	19.26	6.29	1.8	5.3	5.3				
	leaves	8.47	6.40	4.1	28.3	6.5	3.06	12.50	15.50	0.158
Sapindus emarginatus	flushings	16.92	1.46	2.7	13.3	5.4	3.57	3.22	24.40	0.117
	leaves	13.19	2.81	3.0	30.2	11.0	2.62	21.25	20.25	0.102
Alangium salvifolium	flushings	26.22	2.63	10.3	14.8	7.5	3.48	8.00	28.00	0.140
	leaves	16.98	7.68	6.7	21.0	11.6	2.10	24.50	24.00	0.245

motivation according to the chemical composition of the available material. The analysis of food samples selected by primates of Panama (Hladik and Hladik, 1969; Hladik and Hladik, et al., 1971), of Sri Lanka (Hladik and Hladik, 1972) and of Gabon (C. M. Hladik, 1973, 1974) show that all contain compounds of high nutritive value, at least in greater proportion than is found in natural products not selected as food by the monkeys.

Young leaves and shoots eaten by primates often contain more than 20 percent protein (Tables 4 and 5) which may reach 50 percent in leguminous shoots. Mature leaves have only between 7 and 15 percent protein. There is also an obvious difference in the cellulose and total mineral content. Shoots and young leaves contain more phosphorus than do mature leaves. The latter contain more calcium in a proportion higher than the animals need. Sodium chloride is generally not abundant. This may be the reason why some stems showing a high chloride content are eaten in large quantities by folivores, e.g., the petioles of *Musanga cecropioides* and stems of *Hypselodelphis violacea*, which are eaten by chimpanzees (C. M. Hladik, 1974b) and petioles of various *Cecropia* species eaten by howler monkeys (Hladik and Hladik, 1969).

When shoots and young leaves are eaten by folivores, even up to one-half of the locally available leaves, the plant species is not necessarily harmed since this early pruning may stimulate the growth of new shoots and leaf flushes. It costs the plant energy to replace these young leaves, but this is recovered as soon as the new leaves are functional. Conversely, use of the mature leaves by folivores may damage a plant by removing a large part of its photosynthetic and respiratory organs.

Alkaloids

Out of a total of 408 plant species tested, tests for alkaloids were made at first on fresh leaves of 154 species from 61 families of phanerogams and 2 Pteridophytes of Gabon, including the most common ones. The results of our tests show that only 44 species of the 154 tested were negative for alkaloids, and 18 were conspicuously positive. These proportions are very similar to those obtained by Webb (1949, 1952) in Australia. This screening for alkaloids, which was made with Mayer's and Dragendorff's reagents, after aqueous acid extraction, is not strictly selective. Other nonalkaloid substances, such as proteins, betaines, and tannins, may give precipitates, and Dragendorff's reagent also detects cardiotonic glycosides. Field tests made on fresh leaves are generally good guides to the presence of alkaloids, but further confirmation with a careful methodology needs to be conducted in the laboratory (see discussion by Farnworth, 1966).

We repeated these tests on dry herbarium specimens. Tests made on the same material, fresh and dry, sometimes do not yield the same results. Of 254 additional species which were tested using only dry specimens, the relative proportion of negative results is higher (121 species), but the conspicuous positive results are about the same (30 species). The variable results obtained for some species require more investigation.

Alkaloid screenings and chemical analyses have been made on many plant species in the world. Willaman and Schubert (1961) in a worldwide bibliographic survey reported 3,671 species to contain alkaloids, and Smolenski, et al. (1974) found 797 species to be positive out of 3,259 species tested. In a few countries, alkaloid surveys have been made on many of the living plants in various habitats; e.g., in New Guinea (Hartley, et al., 1973), in Congo-Brazzaville (Bouquet, 1972; Bouquet and Fournet, 1975). It appears that in the rain forest the percentage of positive species is not very high. Furthermore, the percentage of crude alkaloid weight is generally low in most of the species. In New Guinea where chemical analyses were conducted (after species were screened in the field for the presence of alkaloids), the results for the characteristic plants of the lowland rain forest were: 18 positive species of a total of 93 tested species (20 percent) with 13 species with less than 0.5 percent (dry weight) and only 5 species between 0.5 to 6.5 percent (dry weight) (Hartley, et al., 1973).

It seems more important, however, to discuss the total biomass of species which contain alkaloids rather than merely species numbers. A preliminary estimate of alkaloid content and its relation to leaf production in a rain forest (Table 6) is given according to our species-by-species leaf-litter analysis. Tree and liana species are listed in decreasing amounts of leaf production by dry weight. The results of the tests concern fresh or dry mature leaves, or both. To complement these data, we added an index of insect folivory for herbarium specimens (there is a bias because the best available plant material has been chosen for herbarium specimens; nevertheless, comparison between species is possible). Comparative data are given from Bouquet's work in the Congo and the Ivory Coast. Alkaloids are distributed without any outstanding difference between tree and liana species; between rare and common species, or between emergent and medium species. Neither is

Table 6.—Alkaloids and other secondary compounds in leaves related to leaf production in the Ipassa forest.

The production shows the relative importance of the different species (by dry weight) collected in 40 sampling baskets (31.8 m^2) during 11 months. Alkaloid tests (Mayer (M) and Dragendorff (D)) were made on fresh material and on herbarium specimens (in parentheses).

Tree species	*Leaf production (g dry weight)*	*Alkaloids tests*		*Insect folivory*	*Comparative data (mostly from Bouquet, et al., 1972, 1974, and 1975)*
		M	*D*		
Panda oleosa	1272	+	+ +	0	Alkaloids in bark and roots
		+	−		
		(−)	(−)		
Scorodophloeus zenkeri	742	−	+?	0	
		(+?)	(+)		
Plagiostyles africana	543	+	+	0	
		(+)	(+)		
Piptadeniastrum africanum	476	−	−	2	Saponins in leaves; alkaloids in bark and roots
		(−)	(−)		
Pentaclethra eetveldeana	152	−	+?	0	Saponins in leaves; alkaloids in bark and roots
		(−)	(−)		
Coula edulis	371	−	−	1	Tannins in bark
		(−)	(−)		
Polyalthia suaveolens	367	+ + +	+ + +	2	Alkaloids in bark and roots
		+ + +	+ + +		
		(+)	(+ +)		
Santiria sp. II	332	−	−		Tannins in bark and roots of *Santiria trimera* s.l.
		(+?)	(+ +)		
Santiria sp. I	92	+?	+?	2	
		(−)	(−)		
Ficus sp. 1744	332	(−)	(−)	0	
Macaranga barteri	313	(−)	(+)	2	
Celtis tessmannii	285	(+ +)	(+ + +)	1	No alkaloids in leaves, but in bark
Petersianthus macrocarpus	274	−	−	0	Tannins in leaves
		(+)	(+)		
Dialium sp. 2142	269	(−)	(−)	3	
Strombosiopsis tetrandra	229	(−)	(−)	2	No secondary compounds
Gambeya beguei	181	+	+	0	No alkaloids
		(−)	(−)		
Pausinystalia macroceras	166	+ +	+ +	0	
		+	+		
		(+ +)	(+)		
Heisteria parvifolia	134	+ +	+ + +	0	Tannins in bark and roots
		(+)	(+)		
Sorindeia nitidula	123	(−)	(−)	1	
Coelocaryon preussii	129	(−)	(−)	2	Saponins and tannins in bark and roots
Ongokea gore	127	(+)	(+)	0	Saponins in leaves
Baphia pubescens	103	(−)	(+)	2	
		( )	( )		
Blighia welwitschii	103	(−)	(−)	0	Saponins in leaves
Eriocoelum macrocarpum	100	(−)	(−)	2	
Anonidium mannii	99	+	+	2	Alkaloids in leaves
		(+)	(+)		

Table 6.—Alkaloids and other secondary compounds in leaves related to leaf production in the Ipassa forest. (Continued)

Tree species	*Leaf production (g dry weight)*	*Alkaloids tests*		*Insect folivory*	*Comparative data (mostly from Bouquet, et al., 1972, 1974 and 1975)*
		M	*D*		
Dialium sp. 1462	88	(−)	(−)	2	
Pycnanthus angolensis	66	(−)	(±?)		No secondary compounds
Alstonia congensis	63	+	+	0	Alkaloids in bark
		(−?)	(−?)		
		(+)	(++)		
Markhamia sessilis	63	(−)	(−)	1	Saponins in leaves; alkaloids in roots
Irvingia gabonensis	58	(+?)	(+)	0	Tannins in bark and roots
Drypetes gossweileri	57	(−)	(+)	2	
Cola rostrata	50	−	−	3	
		(−?)	(−?)		
Lianas species					
Combretum spp.	872	−	−	1	Tannins in leaves of some
		(−)	(−)		*Combretum* species
		(−?)	++		
Neuropeltis acuminata	576	−	+	2	
		(+?)	(++)		
Entada scelerata		(+)	(−?)	0	
Dalhousiea africana	548	(+?)	(+?)	2	
Uvaria sp. 2075	494	(−)	(−)	2	
Tetracera alnifolia	356	(−)	(−)		Flavones in leaves
Cylindropsis parvifolia	343	(−)	(−)	0	
Pycnobotrya nitida	225	−	+?	0	No secondary compounds in
		(+?)	(+?)		bark
Entada gigas	187	+	+?		Saponins in leaves and bark
		(−)	(−)		
Salacia sp. 2589	183	+++	+++		
		(+)	(++)		
Urera cameroonensis	163	−	+		
		(−)	(−)		
Castanola paradoxa	117	(−)	(−)	3	
Dictyophleba stipulosa	107	(−)	(−)	3	
Dichapetalum mombuttense	77	(−)	(−)	0	Alkaloids in roots of other species
Cissus dinklagei	57	−	−		
		(−)	(−)		

there a clear relation between our estimation of insect feeding damage and that of alkaloids in the leaves.

In addition, for a few species, both young and mature leaves were tested. On the fresh material, we obtained more precipitate in the mature leaves than in young ones, but too few species have been tested in this respect. When testing a similar dry weight, the amount of precipitate was either similar or higher in the young leaves. It is difficult to formulate a firm conclusion since proteins are very abundant in young leaves, and may contain precipitate instead of the alkaloids. In any case, in terms of fresh weight, young leaves have more diluted alkaloids and it is likely that they have a low toxicity for most folivorous species.

The presenee of alkaloids and other secondary compounds perhaps has been selected for by the pressure of animals which feed on plants. For example, insects feeding on leguminous seeds may exert selection pressure for the presence of alkaloids (Janzen, 1969, 1971, 1973). The presence of tannins in mature oak leaves may be related to a similar evolutionary process of the plant such as chemical bonding with proteins to prevent digestion by caterpillars (Feeny, 1969, 1970). Other work is currently in progress concerning insect feeding on shoots of Meliaceous trees (Grijpma, 1976). Freeland and Janzen (1974) recently reviewed herbivory in mammals. Unfortunately, data concerning arboreal mammal folivory and leaf toxicity in a rain forest are scarce. It is important, however, to note that most tropical trees which have been tested have larger amounts of alkaloids in bark, roots, or seeds than in leaves (according to the preliminary screenings for alkaloids by Bouquet, 1972, Bouquet and Fournet, 1975). Whittaker and Feeny (1971) defined allelochemics according to their ecological functions, one of which is plant interspecific competition. It is not surprising to find larger concentrations of allelochemics in roots than in leaves where eventual precursors might not be toxic. In temperate regions toxicity by root exudates as well as leaf exudates has been demonstrated (e.g., leachate of *Adenostoma fasciculatum* foliage, Muller and Chou, 1972). In any case, various patterns in alkaloid physiology might exist as suggested by McKey (1974).

Conclusion

In a rain forest, little is known about the specificity of insect leaf folivory. What is known is that the impact of insect folivory on leaf production may reach 10 percent of the total litter-fall (Leigh and Smythe, 1978). For primates and for many other vertebrates, the diet of folivorous species may include a small number of plant species; but two groups of the same folivorous species living in nearby areas may feed on a different set of plant species (Hladik and Hladik, 1972; C. M. Hladik, 1978; Richard, 1973, 1978; Rudran, 1978). Different individual sloths may also have different species of "modal tree" (Montgomery and Sunquist, 1975, 1978). In any case, the impact of the folivorous vertebrate populations is low; they do not eat more than 1 percent of the total leaf produetion of a rain forest (C. M. Hladik, 1978; Montgomery and Sunquist, 1975; Leigh and Smythe, 1978). Because they utilize only a limited set of plant speeies, their distribution is mainly determined by the complementarity of the various leaf phenological patterns of lianas and trees in their various co-cxisting phases of development and growth activity. The plants chosen as food by vertebrates can be related to the composition of the leaves in terms of primary compounds. By contrast, secondary compounds have less influence on vertebrate food choice (see C. M. Hladik, 1978). For invertebrates which are in fact the main consumers (see Leigh and Smythe, 1978), the process of food selection might be different owing to a long history of co-evolution, but further data are still necessary to support the hypothesis concerning insects and leaf co-evolution in rain forests.

Summary

An evergreen tropical forest of Gabon has been studied in terms of its ecology. Profile and projection maps contributed to an analysis of this heterogeneous, species-rich forest. Different ecotopes are described and related to the ecology of the resident vertebrate fauna.

The total leaf litter-fall (6.5 T/ha/year) in the Ipassa forest is similar to other observations in the tropics. It varies throughout the year with a minimum during the major dry season. A climatic pecularity of Ipassa is the lack of direct sunshine in the dry season. Various leaf phenological patterns are shown by different types of tree and liana species. New leaves generally grow at the beginning of each rainy period. Deciduous trees play an important role in the availability of food for leaf-eaters, because they give a localized mass of young leaves at different times of the year. A quantitative estimate of the young leaves available as food is presented.

The toxicity of leaves of tree and liana species in the tropics is still subject to discussion because not enough data are presently available. According to our biochemical analysis of food plants (in different

primate diets of various countries), plant species are chosen according to their richness in nutrients, the young leaves especially showing a greater amount of proteins and soluble sugars than mature leaves.

Literature Cited

Aubréville, A.
1938. La Fôret coloniale: les fôrets de l'Afrique Occidental Française. *Annales de l'Academie des Sciencês Coloniales, Paris,* 9:1-245.
1967. La Foret primaire des montagnes dc Belinga. *Biologia Gabonica,* 3:95-108.

Bernhard-Reversat, F.
1970. Etude de la litière et de sa contribution au cycle des éléments minéraux en forêt ombrophile de Côte d'Ivoire. *Oecologia Plantarum,* 5:247-266.

Blasco, B., and B. Tassy
1975. Etude d'un écosystème forestier montagnard du Sud de l'Inde. *Bulletin d'Ecologie,* 6:524-538.

Bouquet, A.
1972. Plantes médicinales du Congo-Brazzaville. *Travaux et Documents de l'O.R.S.T.O.M.,* 13:1-112.

Bouquet, A., and M. Debray
1974. Plantes médicinales de la Côte d'Ivoire. *Travaux et documents de l'O.R.S.T.O.M.,* 32:1-231.

Bouquet, A., and A. Fournet
1975. Recherches chimiques préliminaires sur les plantes médicinales du Congo-Brazzaville. *Fitoterapia,* 4:175-191.

Cachan, P., and J. Duval
1963. Variations microclimatiques verticales et saisonnières dans la forêt sempervirente de Basse Côte d'Ivoire. *Annales de la Faculté des Sciences de l'Université de Dakar,* 8:5-87.

Catinot, R.
1970. Premieres Réflexions sur une possibilité d'explication physiologique des rythmes annuels d'accroissement chez les arbres de la forêt tropicale africaine. *Bois et Forets des Tropiques,* 131:3-36.

Charles-Dominique, P.
1971. Eco-éthologie des Prosimiens du Gabon. *Biologia Gabonica,* 7:121-228.
1977. *Ecology and Behaviour of Nocturnal Primates.* London: Duckworths.

Farnworth, N. R.
1966. Biological and phytochemical screening of plants. *Journal of Pharmaceutical Sciences,* 55:225-276.

Feeny, P. P.
1969. Inhibitory effect of oak leaf tannins ou the hydrolysis of proteins by trypsin. *Phytochemistry,* 8:2119-2126.
1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by wintermoth caterpillars. *Ecology,* 51:565-581.

Frankie, G. W.; H. G. Baker; and P. A. Opler
1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology,* 62:881-919.

Freeland, W. J. , and D. H. Janzen
1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *American Naturalist,* 108: 269-289.

Gassita, J. N.
1968. Recherches sur quelques plantes médicinales du Gabon. Thèse de pharmacie, Paris.

Gautier-Hion, A., and J. P. Gautier
1974. Les Associations polyspécifiques de Cercopithèques du plateau de N'passa (Gabon). *Folia Primatologica,* 22:134-177.

Grijpma, P.
1976. Resistance of Meliaceae against the shoot borer *Hypsipyla,* with particular reference to *Toona ciliata* M. J. Roem. var. *australis* (F. v. Muell.) C. D.C. Pages 69-78 in J. Burley and B. T. Styles, editors, *Tropical Trees.* Linnean Socicty Symposium Series 2.

Halle, F., and R. Martin
1968. Etude de la croissance rythmique chez l'Hévéa (*Hevea brasiliensis* Muell.-Arg. Euphorbiacees-Crotonoidées). *Adansonia,* 8:475-503.

Halle, F., and R. A. A. Oldeman
1970. *Essai sur l'architecture et la dynamique de croissance des arbres tropicaux.* Paris: Masson et Cie.

Hartley, T. G.; E. A. Dunstone; J. S. Fitzgerald; S. R. Johns; and J. A. Lamberton
1973. A survey of New Guinea plants for alkaloids. *Lloydia,* 36:217-319.

Hladik, A.
1970. Contribution à l'étude biologique d'une *Araliaceae* d'Amérique Tropicale: *Didymopanax morototoni. Adansonia,* ser. 2, 10:383-407.
1974. Importance des lianes dans la production foliaire dc la forêt équatoriale du Nord-Est du Gabon. *Comptes rendus de l'Académie des Sciences, Paris,* série D, 278:2527-2530.

Hladik, A., and C. M. Hladik
1969. Rapports trophiques entre végétation et Primates dans la forêt de Barro-Colorado (Panama). *La Terre et la Vie,* 1:25-117.

Hladik, C. M.
1973. Alimentation et activité d'un groupe de Chimpanzés réintroduits en forêt gabonaise. *La Terre et la Vie,* 27:343-413.
1974a. Géophagie et nutrition minérale chez les Primates

sauvages. *Comptes Rendus de l'Académie des Sciences, Paris,* serie D, 279:1393-1396.

1974b. L'alimentation protéique du Chimpanzé dans son environnement forestier naturel. *Comptes Rendus de l'Académie des Sciences, Paris,* série D, 279: 1475-1478.

1978. Adaptive strategies of primates in relation to leaf-eating. Pages 373-395 in G.Gene Montgomery, editor, *The Ecology of Arboreal Folivores.* Washington, D.C.: Smithsonian Institution Press.

Hladik, C. M., and A. Hladik

1972. Disponibilités alimentaires et domaines vitaux des Primates à Ceylan. *La Terre et la Vie,* 26:149-215.

Hladik, C. M.; and A. Hladik; P. Bousset; P. Valdebouze; G. Viroben; and J. Delort-Laval

1971. Le régime alimentaire des Primates de l'île de Barro-Colorado (Panama). Resultats des analyses quantitatives. *Folia Primatologica,* 16:85-122.

Janzen, D. H.

1969. Seed eaters versus seed size, number, toxicity and dispersal. *Evolution,* 23:1-27.

1971. Seed predation by animals. *Annual Review of Ecology and Systematics,* 2:465-492.

1973. Community structure of secondary compounds in plants. *Pure and Applied Chemistry,* 34:529-538.

John, D. M.

1973. Accumulation and decay of litter and net production of forest in Tropical West Africa. *Oikos,* 24:430-435.

Koriba, K.

1958. On the periodicity of tree growth in the tropics. *Garden's Bulletin of Singapore,* 17:11-81.

Leigh, E. G., and N. Smythe

1978. Leaf production, leaf consumption, and the regulation of folivory on Barro Colorado Island. Pages 33-50 in G. Gene Montgomery, editor, *The Ecology of Arboreal Folivores.* Washington, D.C.: Smithsonian Institution Press.

Lemée, G., and N. Bichaut

1971. Recherches sur les écosystemes des réserves de la forêt de Fontainebleau. 1. Production de litière et apport au sol d'éléments minéraux majeurs. *Oecologia Plantarum,* 6:133-149.

Lim, M. T.

1974. Litter fall and mineral nutrient content of litter in Pasoh Forest Reserve. Kuala Lumpur: IBP Synthesis Meeting.

McKey, D.

1974. Adaptive patterns in alkaloids physiology. *American Naturalist,* 108:305 320.

Medway, Lord

1972. Phenology of a tropical rainforest in Malaya. *Biological Journal of the Linnean Society,* 4:117-146.

Menaut, J. C.

1974. Chute des feuilles et apport au sol de litière par les ligneux dans une savane préforestière de Côte d' Ivoire. *Bulletin d'Ecologie,* 5:27-39.

Montgomery, G. G., and M. E. Sunquist

1975. Impact of sloths on neotropical forest energy flow and nutrient cycling. Pages 69-98 in F. Golley and E. Medina, editors, *Trends in Tropical Ecology. Ecological Studies 11.* New York:Springer-Verlag.

1978. Habitat selection and use by two-toed and three-toed sloths. Pages 329-359 in G. Gene Montgomery, editor, *The Ecology of Arboreal Folivores.* Washington, D.C.: Smithsonian Institution Press.

Montgomery, G. G.; M. E. Sunquist; and T. B. Croat

197 . Liana diversity, tree falls and a view of tropical forest dynamics. *Biotropica* (submitted).

Muller, C. H., and C. H. Chou

1972. Phytotoxins: an ecological phase of phytochemistry. Pages 201-216 in J. B. Harborne, editor, *Phytochemical Ecology.* London:Academic Press.

Oates, J. F.

1974. The ecology and behaviour of the black-and-white colobus monkey (*Colobus guereza* Rüppell) in East Africa. Ph. D. Thesis, University of London.

Oldeman, R. A. A.

1974. Ecotopes des arbres et gradients écologiques verticaux en forêt guyanaise. *La Terre et la Vie,* 28:487-520.

1975. Atlas de la Guyane. Manuscript.

Rapp, M.

1969. Production de litière et apport au sol d'éléments minéraux dans deux écosystèmes méditerranéens: la forêt de *Quercus ilex* et la garrigue de *Quercus coccifera. Oecologia Plantarum,* 4:377-410.

Richards, P. W.

1952. *The Tropical Rainforest.* Cambridge: Cambridge University Press.

Rollet, B.

1969. Etudes quantitatives d'une forêt dense sempervirente de la Guyane vénézuélienne. Thése de Doctorat, Faculté de Toulouse.

1974. *Architecture des forêts denses humides sempervirentes de plaine.* Nogent sur Marne: Centre Technique Forestier Tropical.

Smolenski, J. J., H. Silinis; and N. R. Farnworth

1974. Alkaloid screening. IV. *Lloydia,* 37:30-61.

Struhsaker, T. T., and J. F. Oates

1975. Comparison of the behavior and ecology of red colobus and black-and-white colobus monkeys in Uganda; a summary. Pages 103-123 in R. H. Tuttle, editor, *Socioecology and Psychology of Primates.* The Hague: Mouton.

Webb, L. J.
1949. An Australian phytochemical survey. I. Alkaloids and cyanogenetic compounds in Queensland plants. *Commonwealth Scientific and Industrial Research Organization, Australia, Bulletin No.* 241.
1952. II. Alkaloids in Queensland flowering plants. *Commonwealth Scientific and Industrial Research Organization, Australia, Bulletin No.* 268.

Whittaker, R. H., and P. P. Feeny
1971. Allelochemics:chemical interaction between species. *Science,* 171:757-770.

Willaman, J. J., and B. C. Schubert
1961. Alkaloid-bearing plants and their contained alkaloids. *U. S. Department of Agriculture Technical Bulletin,* 1234:1-287.